

USE OF THE PROBOSCIS FOR PREY-PIERCING AND
SUCKING BY SPHECID WASPS OF THE GENUS *PRIONYX*
(HYMENOPTERA: SPHECIDAE), A CASE OF
CONVERGENT EVOLUTION

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Most sphecid wasps feed mainly on nectar of flowers, sap, exudations or aphid honeydew, which they lick. Some are also known to use body fluids diverted from the prey they catch for their larvae. This supplements their usual diet or perhaps in some cases represents their exclusive diet. *Ampulex* wasps, for instance, have been seen amputating part of both antennae of their paralyzed roach-prey and feeding on the exuding body fluids (Williams and others, *in* Bohart and Menke, 1976, p. 75). Other wasps, such as *Xyllocelia* (Powell, 1963, p. 162) or *Pemphredon* (*in* Bohart and Menke, 1976, p. 180) suck dry some of their aphid prey and do not use them for nesting (also pers. obs.). Still other wasps catch even a different prey for their own consumption. Thus the nyssonine wasp *Stictia signata* (Linnaeus) was observed on the Amazon River feeding on *Aedes aegypti* (Linnaeus) mosquitoes whereas it fed horseflies to its larvae (Howard et al., 1912). *Oxybelus emarginatus* Say captured Diptera much smaller than the usual prey, crushed them and consumed the body fluids (Snoddy, 1968, p. 1030). Many more instances can be found in the literature.

Most sphecid wasps have rather short, unspecialized mouthparts, which can also be used for chewing or crushing prey or opening a hole to extract body fluids. In contrast, many bees have often developed highly specialized and elongate mouthparts, adapted to the exploitation of very specialized flowers, with deep corollas. A few sphecid wasps, notably some bembicine wasps, have evolved similar specializations. *Bembix* and even more so *Steniolia* wasps have a long or very long proboscis they use to exploit flowers with deep or very deep corollas, as hummingbirds and hawkmoths do. In contrast to bees, however, this long, pointed and stiff proboscis can also be used to puncture the Diptera they take as prey and to suck them dry, as robberflies (Asilidae) do. Ferton (1897, 1899, 1902) was one of the first to report such behavior from *Bembix* wasps (*B. oculata* Panzer, *B. rostrata* (Linnaeus)). These prey were never used for nesting. *Microbembex monodonta* (Say) also sucks Diptera (Hartman, 1905, p. 24). Janvier (1928) observed in South America *Bembix brullei* Guérin-Méneville that stabbed

Diptera with the proboscis, on the ventral side of the thorax, in front of the forelegs, sucked them dry and then discarded the remains. Nielsen (1945, p. 32) thinks that such behavior is motivated by thirst, not hunger, as Ferton originally suggested.

Prionyx wasps have a much less elongate proboscis but they can also use it for stabbing, piercing their grasshopper-prey (pers. obs.) in addition to licking nectar in moderately deep corollas. The latter is probably the primary function and the former a derived function. Such stabbing, followed by licking of body fluids, was consistently observed as part of a detailed behavioral study of *Prionyx parkeri* Bohart and Menke, conducted in S.E. Arizona (1972–1973), then in west-central Oregon (1977) and summarized by Steiner (1976). The prey were Acrididae, mainly Oedipodinae, but also some Cyrtacanthacridinae (Steiner, in prep.) taken as adults or last nymphal instars. This behavior usually followed prey stinging and was preceded by a thorough investigation of the latero-dorsal surface of the neck membrane (Fig. 1).

First the wasp was usually seen compressing rhythmically this neck area with the jaws (“kneading,” also observed by Peckham and Kurczewski, 1978, on crickets paralyzed by *Chlorion aerarium* Patton). Then the wasp appeared to stab the neck membrane with the proboscis and started to lap some body fluids deep in the wound, perhaps as deep as the crop. Subsequent examination of such grasshoppers invariably revealed the presence of one latero-dorsal “stabbing wound” on only one side of the neck (Fig. 2). This single wound did not appear to result from the action of the jaws otherwise two more or less symmetrical wounds would be observed, one on each side of the neck. Such symmetrical wounds were found regularly on each side of the foreleg bases of crickets and grasshoppers used as prey by *Liris* and *Tachysphex* wasps, respectively (Steiner, 1962, 1976). These wasps, and also apparently *Larra analis* Fabricius, that preys on *Gryllotalpa hexadactyla* Perty mole crickets (Smith, 1935), performed vigorous chewing motions at the base of these forelegs and then lapped the fluids which oozed from the wounds. For *Liris* wasps, this behavior often occurred right after prey stinging (feeding behavior?) and was consistently repeated inside the burrow (“malaxation”), just before egg-laying. Now, however, the forelegs of the prey were vigorously compressed and at the same time pushed forwards, immediately followed by egg-laying, right behind the forelegs. This second behavior, although superficially very similar to the first one, except for pushing, is therefore no longer feeding but pre egg-laying behavior instead, in other words part of nesting behavior (Steiner, 1962, 1971). In contrast, neck puncturing of the grasshopper by *Prionyx* wasps is not repeated before egg-laying and the oviposition site is no longer located in the same area but at the base of one hind leg. In *Prionyx* it is therefore not pre egg-laying or a “preparation” of the oviposition site. The primary or sole function of this behavior appears to be feeding, absorption of fluids or at least



Fig. 1. *Prionyx parkeri* about to perform "malaxation" behavior on the dorsal side of the neck of an oedipodine grasshopper, shortly after prey-stinging.

sampling of the latter. A somewhat comparable behavior was also observed in other *Prionyx* species, for instance *P. albisectus* Lepeletier and Serville by Roth (1925) and *P. subfuscatus* Dahlbom by Ferton (1902). In the latter case, however, wasp and prey were mouth to mouth, therefore this behavior is perhaps different from the one described in *P. parkeri*. Ferton described this as feeding behavior and thought it was related with a great scarcity of flowers in the arid region considered. Such grasshoppers were discarded and not subsequently used. In the Arizona study of *P. parkeri* 59 instances of neck puncturing were recorded on a total of 44 different grasshoppers (some were punctured several times); the status of 21 other grasshoppers in this respect was unknown and only 5 remaining grasshoppers were known with certainty not to have been punctured. Therefore, the majority of grasshoppers (at least 44 out of 70 and probably many more) were treated in this way. Position of the wound varied relatively little except for an occasional wound located near the median dorsal line rather than latero-dorsally, as shown in Fig. 2.

As an alternative or complementary explanation, this behavior might represent licking up of the defensive fluid often used by the attacked grasshopper and regurgitated through the mouth (Steiner, 1976, also detailed study in prep.). *Prionyx* wasps have been seen lapping up fluids exuding from the



Fig. 2. Paralyzed adult grasshopper (*Psoloessa delicatula* Scudder) showing "stabbing wound" in latero-dorsal neck region, resulting from "malaxation" by a *Prionyx parkeri* wasp.

mouth of the prey (pers. obs.; see also for instance Ferton, 1902; Piel, 1935 for *P. subfuscatus* and Evans, 1958 for *P. atratus* Lepeletier). This fluid has a clear repelling, unpleasant or even deleterious effect on the wasps, when it comes in contact with their body, abdomen tip, during stinging. It triggers vigorous body rubbing and can stop the attack (Steiner, 1976). It might also be noxious for the egg and larva. Conceivably, the wasp might try to eliminate this defense by removing the fluid and lapping it up, from the mouth, or even through the neck wound, internally. The first paralyzing sting in the throat also prevents or stops regurgitation, among other effects, if delivered quickly enough (Steiner, 1976). Besides or instead of feeding, neck puncturing could then have a protective function for the wasp, egg, or both. More research is clearly needed.

Podalonia wasps and their agrotid caterpillar-prey (cutworms) exhibit a very comparable or identical behavior (pers. obs.), namely head-neck "kneading" and/or puncturing with the rather pointed proboscis for the wasp, mouth regurgitation of a defensive fluid for the prey. Lapping of this fluid was also observed, dorsally or ventrally, and also the vigorous body rubbing, even contortions (Fabre's "victory dance"?), following contact of the fluid with the body of the wasp. The compression motions of the jaws have also been interpreted by some as an aid to paralysis, due to better venom diffusion and/or direct mechanical action on the brain. Mole crickets attacked by *Larra* wasps release an even more potent, very viscous, defensive fluid in which the wasps can become entangled (Williams, 1928).

Various "preparations" of prey by sphecid wasps might therefore have a different functional significance and evolutionary origin. In some cases no link with feeding or absorption of fluid is apparent and only a nesting function can be detected. Thus *Oxybelus* and some other crabronine wasps prevent the egg-bearing fly from falling on the side by extending laterally one wing of the prey. This is clearly pre egg-laying behavior but contrary to *Liris* wasps it is apparently completely divorced from feeding or lapping of body fluids.

Like *Liris* and *Tachysphex*, *Prionyx parkeri* wasps do regularly use the prey for nesting, after the neck-puncturing has been performed. Such prey, which are never sucked dry, are not necessarily discarded as Ferton stated for *P. subfuscatus*. Therefore, this treatment must be compatible with satisfactory preservation of the prey and successful nesting, otherwise wasps using such prey would probably have been selected against. Of the 44 punctured grasshoppers, 23 were subsequently used for nesting (these wasps store only one prey per nest). The remaining 21 were not used, but not necessarily because they had been punctured, since some non-punctured ones were also discarded. A meaningful comparison of nesting success of punctured vs. non-punctured grasshoppers is difficult in this study, however, first because no special effort was made to raise the larvae in optimal conditions, second too many grasshoppers were of unknown status because they were stored before their neck area could be checked. At any rate here are the inconclusive results: a total of 21 nests with punctured grasshoppers and 14 of unknown status or non-punctured grasshoppers were dug up. Two nests of each category were destroyed accidentally, leaving 19 and 12, respectively. Nesting success was as follows; larvae that reached maturity and spun a cocoon: 5 (=26.3%) vs. 4 (=33.3%), respectively; adults produced the next year: 3 (=15.8%) vs. 1 (=8.33%). Clearly these numbers are too small to warrant reliable conclusions. It is clear, however, that neck-puncturing is compatible with nesting success and did not reduce the latter drastically, when compared with the other category.

In conclusion, apparent derivation of prey-piercing behavior from nectar-licking behavior by evolution of a stronger, more specialized, piercing proboscis, as seen in some sphecid wasps (particularly *Bembix*), occurred at least once more, in another group of unrelated insects, namely a few fruit-piercing and skin-piercing (blood-sucking) noctuid moths (Bänziger, 1971, 1975). They must also have evolved from the more common nectar-feeding forms, with a non-piercing proboscis. This is apparently a case of convergent evolution.

Furthermore, at least one sphecid wasp, *Oxybelus emarginatus*, is known to lick blood droplets from the cattle exposed to their blood-sucking (simuliid) fly prey (Snoddy, 1968). They do not, however, pierce the skin of the cattle like the blood-sucking moths do. The latter might well have gone through a similar stage of dependence from blood excreted by mosquitoes before becoming able to pierce the skin themselves (Alcock, 1975, p. 401).

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